

Foraging Behavior and Colony Cycle of *Agelaia vicina* (Hymenoptera: Vespidae; Epiponini)

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Abstract.—The neotropical *Agelaia vicina* has the largest nest built among social wasps, yet little is known about nest construction, growth and structure. In this work, the development of two nests of *A. vicina* was followed. Studies were done through analysis of images to estimate the growth of nests. The material collected below the nests was examined to estimate colony productivity. Nests were collected to analyze their architecture and structure. Colony cycle was similar in the two colonies. Colonies increase in size throughout the dry season and into the rainy season, with a sudden drop in production at the end of the rainy season. The colonies doubled in size in about six months.

Social wasps are important to the study of social evolution. They fall into two groups according to how they initiate colonies (Jeanne 1991). In independent-founding species, one or a small group of queens start the construction of a new nest, without the aid of workers. In swarm-founding species, a new colony is initiated by a large group of workers and one or more queens. Patterns in nest construction vary. The independent-founders are characterized by continuous nest construction; that is, the size of the nest increases gradually throughout the founding and ergonomic stages of the colony cycle, and is closely correlated with oviposition rate (Richards and Richards 1951; Wenzel 1991).

In contrast, some several swarm-founding species engage in episodic nest construction, building the nest rapidly at the beginning of the founding stage. The new cells are constructed faster than the queens fill them with eggs. The nest is completed rapidly in this stage (Jeanne 1991; Wenzel 1991), and then the nest stays static for weeks or months, while the colony expands its population within the limits of its

initial structure. Subsequent expansion of the nest in its following stage is equally quick, building hundreds or thousands of cells in a few days.

In tropical environments, the groups most studied for foraging behavior are *Polistes*, *Mischocyttarus*, and *Polybia* (Dapporto and Palagi 2006; Hermann and Chao 1984; Hrncir et al. 2007; Jha et al. 2006; O'Donnell and Jeanne 2002; Richter 2000). The importance of these wasps is related to how they act in a trophic network as herbivores (sugar and nectar collectors) and predators (Raposo Filho and Rodrigues 1983). Necrophorus feeding habits are known in *Agelaia* and *Angiopolybia* (O'Donnell 1995). *Agelaia* is very commonly found at flowers (Mechi 2005) and is among the most abundant genera in neotropical forests (Hunt et al. 2001; Silveira et al. 2005; Zucchi et al. 1995), indicating its ecological importance.

Agelaia vicina (Saussure) has the largest colony size among the social wasps. Von Ihering (1903, 1904) first offered information on this, reporting an *A. vicina* colony of with more than 108,000 individuals, but colonies may exceed one million adults

(Zucchi et al. 1995). The nests are built commonly in cavities, such as caverns or tree hollows. Built in protected places, they lack a nest envelope, as in many other *Agelaius* (Hunt et al. 2001; Wenzel 1991). The nest of *A. vicina* is composed of vegetable fibers without wax or resin. Some parts, such as the pedicels receive additional glandular secretion as a presumed reinforcement (Wenzel 1998). Workers build cells that form combs. During nest initiation, several combs are built separately, fixed by pedicels to the substrate (generally ceilings of cavities), so that the combs are parallel to the substrate. The combs are then expanded and merge to form a great expanse of cells. Besides the considerable amount of information regarding nest architecture in *A. vicina*, virtually nothing is known about its biology.

MATERIALS AND METHODS

We observed two nests in São Paulo state, Brazil, one in the municipality of Paulo de Faria Brazil (19°S 49°W) and the other in Pindorama (21°S 48°W). The Paulo de Faria nest was located in an abandoned wooden guard station, 3.5 m above the ground. The Pindorama nest was 2.5 m above the ground, inside a brick structure in the form of a shut tower in the back yard of an abandoned house.

Images were captured using a digital camera in order to measure nest growth. The images of the Paulo de Faria nest were captured from November 2005 to April 2006, those of the Pindorama nest from June 2006 to February 2007. Nest growth was estimated by Axiovision, software that calculates area increase from the images.

At the end of the observations, each nest was collected, weighed and dismantled comb by comb for a better understanding of its structure and composition (Fig. 1A–B). The Paulo de Faria nest was collected after natural decline, and the Pindorama nest was killed for collection. Subsequently, the combs of each nest were cut out in squares with areas of 100cm². We

used these squares for counting and weighing nest cells.

In February 2007 we gathered 42 hours of video segments at the entrance of the Pindorama nest in order to record the departure and return of foragers. These images were studied then in slow motion. We recorded for one hour each at starting times of 06h, 14h, 18h and 24h.

To study foraging behavior, we offered baits of meat 15m from the nest. Arriving foragers were marked on the thorax with non-toxic ink. This allowed us to estimate round-trip times. To determine whether the presence of baits increases the number of workers leaving the nest, we noted the number of marked foragers present throughout the day. We designated the start of foraging when the first forager arrived in the bait.

It is known that *A. vicina* discards leftover food and the opercula of pupal cocoons below the nest (Zucchi et al. 1995). Because each operculum corresponds to an emergent adult, the number of opercula corresponds to the number of adults produced in a period of collection. Plastic trays were put below the nests in order to collect the discarded material (Fig. 1C).

RESULTS

Nest growth was continuous during the period of observation. From the image analyses, the Paulo de Faria nest initially had 459,143 cells, which increased to approximately 956,340 cells over the course of six months of observations, an increase of 108%. After nest collection, it weighed 13.8 kg with cells (or combs) organized in 28 layers (Fig. 1B), yielding an estimate of 69,300 cells per kg. Only the central area (about 30%) of the nest was used for the brood production, as seen in the presence of meconia in these cells. For the nest studied in Pindorama it was not possible to estimate nest growth. When the nest was collected, it had approximately 745,564 cells distributed in 41 layers and weighed 11.5kg (Fig. 1A). As in the Paulo de Faria



A



B



C

Fig. 1. Nests of *Agelaia vicina* from Pindorama (A) and Paulo de Faria (B), SP, Brazil. Position of trays beneath a nest to collect material discarded from the Paulo de Faria nest (C).

nest, a central area comprising about 30% of the nest was used for brood production. This nest had about 64,832 cells per kg.

Foraging began early from the Pindorama nest, so that during the 06–07h period when the colony was in an active phase too many workers were active to allow their number to be estimated, even with slow-motion playback (Table 1). Later, in the declining phase of the colony cycle, with fewer individuals and less activity, it was possible to identify more foragers exiting than returning. From 14h–15h to 18h–19h, there were more foragers returning. We observed that about 30% of the “foraging activity” was related to very brief absences that presumably brought nothing into the nest. This behavior gave rise to a cloud of workers outside the nest throughout the

day while the colony was in an active phase.

Foraging times of exiting the nest, arriving at the bait, then returning to the nest in Paulo de Faria averages 2 min (1.19–3.47 min). The increase in the number of foragers in the baits was linear (Fig. 2), suggesting the absence of recruitment (Hrncir et al. 2007).

In October 2005, the colony of Paulo de Faria was active, producing males and workers, both of which are easily identified in this species. Using operculum numbers, we found a rise in the production of new individuals in the period from November 2005 to March 2006, reaching a peak in March, following by a decrease in April 2006 (Fig. 3A), with signs of nest desertion due to the absence of workers in the

Table 1. Mean ratio of *Agelaia vicina* foragers exiting by those returning per minute (values reported as exit/return) in different periods of the day at nest in Pindorama, SP, Brazil. These are recorded both when the colony was active and in apparent good health and later when it was in a state of decline.

	06h~07h	14h~15h	18h~19h	24h~01h
Active	>1000	53/73	150/145	00/00
Declining	30/11	03/06	07/04	00/00

external area of the nest. In front or above the nests of *A. vicina* we sometimes saw a cloud of foragers flying near the nest. This cloud disappeared after April 2006.

The colony cycle at Pindorama was similar to that from Paulo de Faria. From May to June 2006, there was little activity and almost no production of new individuals. After July 2006 males were found in the population. Adult production increased to a climax in January 2007, remained high up to the end of February (2007) when the population lessened drastically (Fig. 3B).

Agelaia vicina collects at least 10 different orders of insects: Lepidoptera, Coleoptera, Dermaptera, Hymenoptera, Heteroptera, Mantodea, Diptera, Neuroptera, Blattodea and Homoptera. In addition, we found

many spiders (Arachnida: Araneae). In the two studied colonies, the taxonomic composition of the discarded prey parts was similar. Lepidoptera and Coleoptera, represented by remains of larval mandibles and adult body parts, were the most common. Spiders were also an important item in their diet. The other orders were found at much lower levels. In addition, we found two different seeds, one from a grass (*Panicum sp.*) and a *Cyperus sp.* Several balls of plant leaf hairs were found, wasp larvae, and some small pebbles and sticks.

DISCUSSION

Information on architecture of the observed nests corroborates that of Wenzel (1991) and Zucchi et al. (1995), in that the

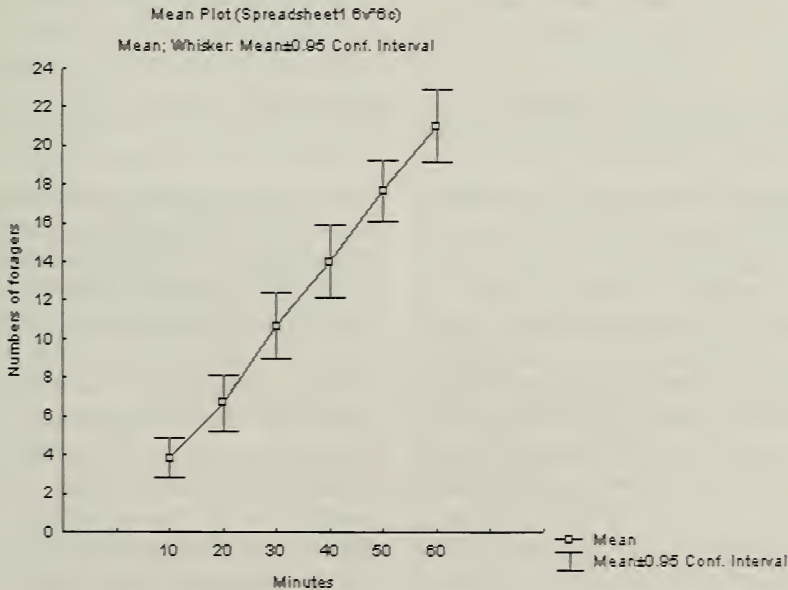


Fig. 2. Numbers of *Agelaia vicina* foragers per minute (mean ± SE) that found and collected meat baits at Pindorama, SP, Brazil.

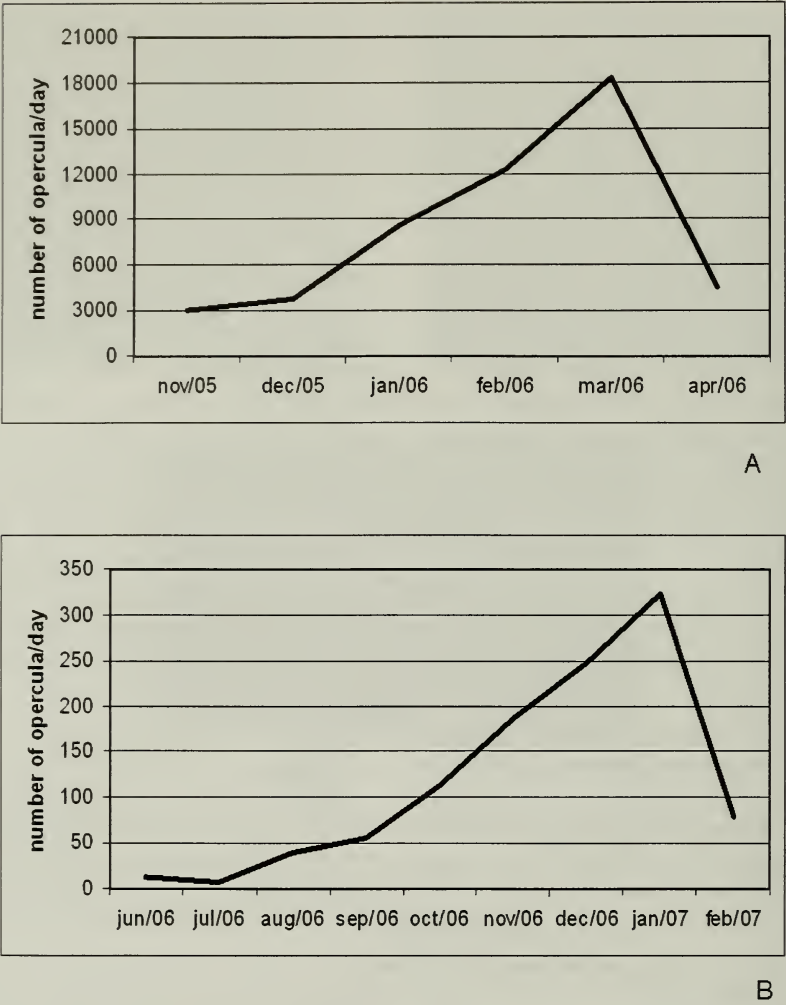


Fig. 3. Number of opercula/day collected during the months of study from nests of *Agelaia vicina* at Paulo de Faria (A) and Pindorama (B), SP, Brazil.

peripheral regions of combs do not fulfill a reproductive function but the act as an envelope. Detailed studies of nest development in swarm-founding wasps are largely limited to the genus *Polybia* (Jeanne and Bouwma 2004; Kudô et al. 2003, 2005; Loope and Jeanne 2008), which provides a baseline for comparison. In swarms of *P. occidentalis* (Oliver), for example, rapid construction in the founding stage completes the initial nest in two to three weeks, followed by almost no change during much of the ergonomic stage. Renewed expansion may occur several weeks or months later (Jeanne and Bouwma 2004).

In *A. vicina*, initial construction of the nest can also be considered rapid, with the construction of several combs. Approximately fifteen pedicels and initial cells may be built in the first five hours (Oliveira pers. obs). However, *A. vicina* then shows a continuous increase in the size of the nest, rather than alternating periods of stasis and sudden expansion. The growth rate found here shows that nests double in size in six months. Factors that allow nests of the great size of *A. vicina* include high growth rate, high population and large number of queens. The large number of foragers producing a cloud of workers during the whole

activity period of the colony is visually impressive. As we observed, most exits from the nest lead to very short flights that appear unconnected with foraging. Hypotheses to explain this persistent cloud include that it a) serves a defensive function in obstructing the approach of predators or parasites, b) serves as a landmark in the orientation of returning foragers, or c) is simply a way of reducing crowding inside the nest during the active part of the day. The absence of feces on the substrate near the nest indicates that these are not defecation flights, as Richards (1978) suggested. If it is found that the cloud is composed of young workers who are not yet fully mature, this would be inconsistent with hypothesis (a) and consistent with (b) and (c).

No recruitment to meat baits was detected. This is in agreement with previous observations on *Agelaia* (Jeanne et al. 1995) and contrary to what was observed for *Polybia paulista* (Ihering) (Hrnčir et al. 2007) in which authors found recruitment for sugar sources. In terms of diet, our results are similar to that from many other social wasps (Edwards 1980). *A. vicina* has a very broad diet, foraging for water (O. Oliveira pers. obs), plant tissues, proteins and carbohydrates. They use plant fibers (cellulose) for nest construction, proteins (from captured arthropods and carrion) and sugar from fruits (probably from the pulp of the seeds found) as energy source for the brood and adults (Akre 1982; Rossi and Hunt 1988; Spradbery 1973). *A. vicina* is a generalist predator of land arthropods, taking spiders and a broad range of insects. We can infer that it plays important roles in their ecosystem as a predator of large numbers of invertebrates (see daily productivity, below).

The colony cycle of the two studied colonies of *A. vicina* was similar. In the dry season, population increases possibly indicated preparations for reproductive swarming, which causes an abrupt fall in colony size, as is known in other Epiponini

(Jeanne 1991). Based on Figure 3A–B, nests differ greatly in the number of individuals produced. The Paulo de Faria nest reached a production of 18,000 new individuals per day, but the Pindorama nest reached no more than 300 individuals per day at peak production. It is hard to account for this very large difference.

For less complex societies, like *Polistes*, feeding efficiency may not to be a limiting factor for nest size (Strassmann and Orgren 1983). In *A. vicina*, however, the fall in worker production may be a consequence of the difficulty of obtaining food in the rainy season, associated with the implications of a high relative moisture for the maintenance of the colony, an increase in predation, or appearance of fungus or parasitism (Hunt et al. 2001; Richards 1978). Because the forest remnant of Paulo de Faria (435 ha) is larger than that of Pindorama (128 ha), it may also provide more resources. Nevertheless, the differences presented regarding the production of new individuals may not be tied only to resource availability but also may relate to the differences in colony age and predation.

The term “keystone species” was coined by Paine (1969). A keystone species influences several organisms in an ecosystem with a effects on the other species out of proportion to its abundance. A keystone species may determine the types and numbers of various other species in a community. Several aspects of our results suggest that *A. vicina* may act as a keystone species. *A. vicina*, besides having the largest nests and colonies among social wasps, has a very high rate of brood production (up to several thousand individuals per day). The quantity of prey brought to the nest is evidently very substantial, especially if we take into account the rough rule of a 10% efficiency energy transfer between trophic levels. *A. vicina* preys upon an impressive diversity of arthropods and must impact their populations locally. We propose *A. vicina*

as a candidate keystone species, so that it would be fruitful if future studies were to evaluate its influence in neotropical environments.

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LITERATURE CITED

- Akre, R. D. 1982. Social wasps. Pp. 1–105 in: Hermann, H. R. ed. *Social Insects*, vol. 4. Academic, New York.
- Dapporto, L. and E. Palagi. 2006. Wasps in the shadow: Looking at the pre-hibernating clusters of *Polistes dominulus*. *Annales Zoologici Fennici* 43: 583–594.
- Edwards, R. 1980. *Social Wasps: Their Biology and Control*. Rentokil, East Grinstead. 398 pp.
- Hermann, H. R. and J. T. Chao. 1984. Nesting Biology and Defensive Behavior of *Mischocyttarus* (*Monocyttarus*) *mexicanus cubicola* (Vespidae: Polistinae). *Psyche* 91: 51–65.
- Hrncir, M., S. Mateus, and F. S. Nascimento. 2007. Exploitation of carbohydrate food sources in *Polybia occidentalis*: social cues influence foraging decisions in swarm-founding wasps. *Behavioral Ecology and Sociobiology* 61: 975–983.
- Hunt, J. H., S. O'Donnell, N. Chernoff, and C. Brownie. 2001. Observations on two neotropical swarm-founding wasps *Agelaia yepocapa* and *A. panamaensis* (Hymenoptera: Vespidae). *Annals of the Entomological Society of America* 94: 555–562.
- Ihering, R. Von. 1903. Contributions à l'étude des Vespides de l'Amérique du Sud. *Annales de la Société Entomologique de France* 72: 144–155.
- . 1904. As vespas sociaes do Brasil. *Revista do Museu Paulista* 6: 97–309.
- Jeanne, R. L. 1991. The swarm-founding Polistinae. Pp. 191–231 in: Ross, K. G., and R. W. Matthews eds. *The Social Biology of Wasps*. Cornell University Press, Ithaca.
- and A. M. Bouwma. 2004. Divergent patterns of nest construction in eusocial wasps. *Journal of the Kansas Entomological Society* 77: 429–447.
- , J. H. Hunt, and M. G. Keeping. 1995. Foraging in social wasps: *Agelaia* lacks recruitment to food. *Journal of the Kansas Entomological Society* 68: 279–289.
- Jha, S., R. G. Casey-Ford, J. S. Pedersen, T. G. Platt, R. Cervo, D. C. Queller, and J. E. Strassmann. 2006. The queen is not a pacemaker in the small-colony wasps *Polistes instabilis* and *P. dominulus*. *Animal Behaviour* 71: 1197–1203.
- Kudô, K., R. Zucchi, and K. Tsuchida. 2003. Initial nest development in the swarm-founding paper wasp, *Polybia paulista* (Hymenoptera: Vespidae, Epiponini): cases of building multiple initial combs. *Journal of the New York Entomological Society* 111: 151–158.
- , S. Tsujita, K. Tsuchida, W. Goi, Sô. Yamane, S. Mateus, Y. Itô, S. Miyano, and R. Zucchi. 2005. Stable relatedness structure of the large-colony swarm-founding wasp *Polybia paulista*. *Behavioral Ecology and Sociobiology* 58: 27–35.
- Loope, K. J. and R. L. Jeanne. 2008. A test of adaptive hypotheses for rapid nest construction in a swarm-founding wasp. *Insectes Sociaux* 55: 274–82.
- Mechi, M. R. 2005. Comunidade de vespas Aculeata (Hymenoptera) e suas fontes florais. Pp. 256–265 in: Pivello, V. R., and E. M. Varanda eds. *O Cerrado Pé-de-Gigante: Ecologia e Conservação - Parque Estadual Vassununga*. Secretaria do Meio Ambiente, São Paulo.
- O'Donnell, S. 1995. Necrophagy by neotropical swarm-founding wasps (Hymenoptera: Vespidae; Epiponini). *Biotropica* 27: 133–136.
- and R. L. Jeanne. 2002. The nest as fortress: defensive behavior of *Polybia emaciata*, a mud-nesting eusocial wasp. *Journal of Insect Science* 2: 3–5.
- Paine, R. T. 1969. A note on trophic complexity and community stability. *American Naturalist* 103: 91–93.
- Raposo Filho, J. R. and V. M. Rodrigues. 1983. Comportamentos tróficos de *Mischocyttarus* (*Monocyttarus*) *extinctus* Zikán, 1935 (Polistinae, Vespidae). I. Alimentação proteica. *Naturalia* (São Paulo) 8: 101–104.
- Richards, O. W. and M. J. Richards. 1951. Observations on the social wasps of South America (Hymenoptera Vespidae). *Transactions of the Royal Entomological Society of London* 102: 1–170.
- . 1978. *The Social Wasps of the Americas, Excluding the Vespinae*. British Museum (Natural History), London. 580 pp.
- Richter, M. R. 2000. Social wasp (Hymenoptera: Vespidae) foraging behavior. *Annual Review of Entomology* 45: 121–150.
- Rossi, A. M. and J. H. Hunt. 1988. Honey supplementation and its developmental consequences: evidence for food limitation in a paper wasp, *Polistes metricus*. *Ecological Entomology* 13: 437–42.
- Silveira, O. T., M. C. Eposito, J. N. Santos Jr, and F. E. Gemaque Jr 2005. Social wasps and bees captured in carrion traps in a rainforest in Brazil. *Entomological Science* 8: 33–39.

- Spradbery, J. P. 1973. *Wasps: an Account of the Biology and Natural History of Social and Solitary Wasps*. University of Washington Press, Seattle. 408 pp.
- Strassmann, J. E. and C. F. Orgren. 1983. Nest architecture and brood development times in the paper wasp *Polistes exclamans* (Hymenoptera: Vespidae). *Psyche* 90: 237–248.
- Wenzel, J. W. 1991. Evolution of nest architecture. Pp. 480–519 in: Ross, K. G., and R. W. Matthews eds. *The Social Biology of Wasps*. Cornell University Press, Ithaca.
- . 1998. A generic key to the nest of hornets, yellowjackets, and paper wasps worldwide (Vespidae: Vespinae, Polistinae). *American Museum Novitates* 3224: 1–39.
- Zucchi, R., S. F. Sakagami, F. B. Noll, M. R. Mechi, S. Mateus, M. V. Baio, and S. N. Shima. 1995. *Agelaiia vicina*, a swarm-founding polistine with the largest colony size among wasps and bees (Hymenoptera: Vespidae). *Journal of the New York Entomological Society* 103: 129–137.